The Geographical Distribution of the Frankeniaceae considered in connection with their Systematic Relationships.

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I.

Introduction, and preliminary discussion of the Systematic, Morphological and Anatomical features of the Frankeniaceae.

Introductory.

The numerous contributions of recent years concerning the influence upon plant growth of the various physical agencies, e. g. the quality of the soil, exposure to extremes of temperature, to scarcity of moisture, to intensity of light, — in short concerning the whole category of environmental conditions, — have increased the desire to discover what has been the history of phylogenetic groups as related to the conditions under which they grow. More particularly is this true in the case of those which occur in conditions of extreme severity as in the xerophytic, but especially the halo-xerophytic groups. Where a large order, as for example the *Chenopodiaceae*, has become so thoroughly identified as halophytic, occupying all of the salt-steppes of the earth, the case is of peculiar interest, because in the first place, of the time involved on the side of the plants to attain to this adaptation, and in the second place because salt-steppe regions are regarded as comparatively recent-geological formations, and therefore it is supposable that in an age not so far removed, the position and extent of salt-steppe deserts was necessarily very different than at present, and consequently the distribution of plants at that time identified with such lands was correspondingly different than that of the same groups or their progeny of today.

This makes a reasonable hypothesis upon which to account for the distribution of plants in salt desert regions so widely separated by impossable barriers of ocean, or mountains, or luxuriant tropics, that no known means is sufficient to account for a transportation of the seeds between the regions as they now are. An interesting illustration occurs in the *Frankeniaceae*. A certain section, *Basigonia*, contains four members distributed as follows. 1. West-Australia. 2. Salt-steppes of Argentine. 3. Lower California. 4. Eastern base of the Rocky Mountains. A direct transportation of seeds between these regions seems impossible. To suppose that in an earlier age salt-steppe regions permitted a wide distribution of a type from which these forms could be derived, is reasonable, provided, of course, the facts of genetic relationship harmonize with this supposition.

If a reason be sought for presenting the small group of *Frankeniaceae* under the title above given, it lies in these two facts. 1. That they occupy, or are represented in nearly all of the salt-steppe regions of the earth, and are without exception dwellers in salt soils. 2. That they are sharply distinguished from groups of plants which are not halophytic.

It seemed both interesting and profitable therefore, to enter into a detailed account of the genetic relationships and the phenomena of distribution in this family, because, having, to all appearance, been identified through a long time with the kind of region in which we find them, these facts might be expected to stand in an instructive relationship to the phylogenetic history of the family.

Systematic.

The *Frankeniaceae* were first presented in full in their systematic order by Niedenzu in »Pflanzenfamilien« to which publication the reader is referred for a comprehensive discussion of the family. The present article will use this arrangement as the basis for discussion, offering only such emendations as seem warranted by a careful study of the family in the light of previous research and with additional material for examination.

As defined in »Pflanzenfamilien« the *Frankeniaceae* are comprised in the four genera *Frankenia* L., *Hypericopsis* Boiss., *Beatsonia* Roxb. and *Niederleinia* Hieron. To these is to be added a fifth, *Anthobryum* Phil.[1]) which is referred to the *Frankeniaceae* by Reiche and Johow, Flora de Chile I. 1896. Concerning the first three genera, there has been a tendency on the part of botanists to combine these in the one genus *Frankenia*, and if we regard only the floral characters, this could appropriately be done, including *Niederleinia* as well (likewise *Anthobryum*). But two

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1) Viaje a la Prov. de Tarapaca (1891) p. 51; *A. tetragonum* Phil. l. c. Pl. II Fig. 3. *A. aretioides* l. c. Fig. 4. These forms will be discussed with *F. triandra* Remy under South American species, sect. *Isolata*, the Puna Region.

other factors, namely, the plant habit and the geographical distribution, unite with floral characters in making it desirable to retain these genera, at least for the purpose of emphasizing certain pronounced lines of developement, notably in *Niederleinia*, and extremes of isolation, notably in *Beatsonia*. But in thus emphasizing certain types, it must not be forgotten that there are other types properly comprehended in *Frankenia* which are scarcely less significant, e. g., *F. bracteata* Turcz., *F. glomerata* Turcz. from Australia, *F. triandra* Remy, Puna Region.

Morphological.

In typical *Frankenia* the floral members may be represented by the formula $K5 - C5 - A6\,(3+3?) - G3$. The number of members in each whorl is however subject to variation even in the genus *Frankenia*, e. g., *F. revoluta* Forsk. varies to $K5 - C5 - A8 - G3$; *F. Boissieri*, generally typical, may have $K5 - C5 - A5$ (single whorl) $- G3$; *F. glomerata* Turcz. $\left\{ \begin{matrix} K\ C\ A\ G \\ 5-5-4-3 \\ \text{or} \\ 4-4-4-3 \end{matrix} \right.$; *F. triandra* Remy, $K5 - C5 - A3$ to $6 - G3$; *F. Palmeri* Wats. $K5 - C5 - A4$ or $G2$; *Hypericopsis* $K6$ or $7 - C6$ or $7 - A20$ or more $- G4$; *Beatsonia* $K5 - C5 - A5$ (single whorl) $- G3$; *Niederleinia* $K5 - C5$ $\left\{ \begin{matrix} - A6 \text{ sterile} - G3. \\ -^{\text{or}} A6 - G3 \text{ sterile}. \\ -^{\text{or}} A6 - G3? \end{matrix} \right.$

From the above instances the number of stamens would seem too variable to be used as a generic character. That there are normally two isomerous whorls seems questionable both because of the common variation, and because often four, five or six stamens are found united below into a cup in which no distinction of outer and inner members can be made. That there are three longer and three shorter, seems a device for economising space for developement in the narrow calyx tube, for example in *F. glomerata*, which has almost filiform calyces. The four stamens are all of different lengths, the anthers, therefore, developing without crowding each other. A more exact method of determining the number of whorls should be employed, however, before the question is pronounced upon finally.

The corolla possesses the ligulate appendage in almost every member of the family, generally well marked, — in *F. triandra* almost a double corolla —, but very indistinct in *Beatsonia*, often very plainly evident in *Niederleinia*, and not at all to be delected in the narrow flowered *F. glomerata*. The number of seeds produced in each capsule varies from one or two in some of the narrowly endemic forms to more than twenty in the widely distributed species. The characteristics which are of value in promoting a wide distribution are: 1. The seeds are very small oval or oblong grains. 2. They are richly furnished with mealy endosperm which

surrounds the embryo. 3. They retain their vitality at least for a period of years [1]).

Anatomical.

The *Frankeniaceae* offer some of the most extreme types of xerophytic structure, although generally growing near salt lagoons where more or less moisture is present in the soil. The presence of the salt is of itself sufficient to cause the plant to assume a xerophytic habit, as is well known, but aside from this, and notwithstanding the presence of moisture in the soil, the plants are exposed to all the extremes of temperature, intensity of sunlight and dryness of air characteristic of the most arid regions. The so-called extreme types have arisen as the result of the different methods of adaptation to these extreme conditions. This is expressed in the whole plant structure, but more particularly in the leaves, in whose form and function, occurence on the stem, in the epidermal structure, arrangement of palissade cells and mechanical tissue, lie characters useful in distinguishing certain species. But any attempt to make a detailed classification of species based on the leaf anatomy, such for instance as proposed by Vesque [2]), results in bringing together species the most widely separated genetically.

In the sections *Eufrankenia* and *Toichogonia cosmopolita*, i. e., those groups referred to in the following pages as the modern developement of the family, the leaves throughout, are of the same general type and occur in the same manner on the stem. In these and all other members of the family, excepting possibly *F. triandra*, the flower is subtended and partially enclosed by the last four leaves, which grow together to form a cup, thus leaving no interval between the two upper pairs of leaves.

The presence of the so-called salt glands is one of the most noteworthy features in the special adaptations of the *Frankeniaceae*. These glands are found without exception in the epidermis of the assimilative structures of every species. Doubtless they furnish one of the most distinguishing characters of the family [3]).

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1) I have planted seeds which had been in the capsules of herbarium specimens for ten years, of which more than 50 % germinated.

2) Contributions a l'histologie systematique de la feuille des Caryophyllinées. Ann. Sc. Nat. Ser. VI Tom. 15 p. 119.

3) On the function of these glands see »Pflanzenfamilien« III 6 S. 290; Volkens, Flora der ägyptisch-arabischen Wüste; Marloth, Berichte d. deutsch. botan. Gesellschaft 1887 S. 319; Stahl, Bot. Zeitung 1894 S. 139. Later I hope to offer the results of my study upon the mechanism of these glands. I can not forbear to suggest here, that the presence of these glands in precisely the same manner in all the genera of *Tamaricaceae*, excepting the North American *Fouqueriae* indicates even a closer relation of this family with the *Frankeniaceae* than has been previously suggested, — a fact which is given probably greater value when one considers

II.

The Geographical Regions with their respective Species considered in detail.

For the purpose of emphasizing the value of the geographical factor in the following pages, the geographical regions will form the main headings under which the species will be presented in their respective groups.

1. The Mediterranean Region.

The *F.* of the Mediterranean Region embrace *Frankenia* Subgen. *Afra*, and the genus *Hypericopsis*.

Eufrankenia.

Eufrankenia (incl. *Protofrankenia* Ndz.) will be taken as typical for the family, with the understanding that it is not thereby designated as the parent group, or even that it bears evidence of so great age as other groups. But that it has retained more nearly the type of the ancestral form appears supported by the fact that in species the most isolated geographically and the most pronounced in vegetative structure the floral structure of *Eufrankenia* is the one most regularly recurred to, — e. g., *F. triandra* Remy, and *Beatsonia*.

Sect. *Eufrankenia*, while embracing some ten or twelve tolerably clearly distinguished forms, is with difficulty divided into well-defined species because of the constant overlapping of forms. This is a feature likewise characteristic of the corresponding sections in Australia and the Western Hemisphere, and is not without its significance in pointing out the relative age of sections *Eufrankenia* and *Toichogonia cosmopolita* to sections *Toichogonia isolata* and *Basigonia*, being one of the chief reasons for calling the former the modern developement of *Frankeniaceae*, in this article.

As the purpose of the present study is not to offer a final revision of species, it must suffice to point out the recognisable forms and their geographical limits, remarking here that where as in »Pflanzenfamilien« some nine species are pretty clearly defined, chiefly on anatomical characters, in Boiss. Fl. Orient. I p. 780, and in the Kew-Index the view is preferred of including all the species embraced in Sect. *Eufrankenia* (excepting *F. pulverulenta*) as varieties under the oldest (?) name *F. hirsuta* L.

The following synopsis includes the more prominent forms:

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the present condition of the *Tamaricaceae* in their geographic-genetic relationships. That *Fouqueria* should be considered one of the *Tamaricaceae* by any close genetic tie, seems not very long tenable.

1. The almost cosmopolitan, fleshy leaved annual *F. pulverulenta* L.

2. The very variable shrubby perennials embracing:

(1) *F. laevis* L. the common prostrate shrubby species of the western Mediterranean countries, extending east to Greece and Crete (incl. var. *intermedia* = *F. intermedia* DC.); north through Spain and France to England; south to Senegambia the Cape Verde and Canary Islands (incl. *F. ericifolia* C. Sm. and *F. capitata* Webb et Bert.), also to Capland. Eastward this species is replaced by

(2) *F. hispida* DC., the common form of the Eastern Medit. countries, from the Balkan Peninsula eastward over the basins of the Black, Caspian and Aral seas, becoming var. *erecta* Boiss. in south-eastern Persia and Afghanistan.

The three following narrowly endemie species:

(3) *F. revoluta* Forsk. in Northern Egypt about Alexandria (eastward in Syria?) distinguished by its capitate stigmas.

(4) *F. velutina* DC. north-east coast of Marocco; peculiar in forming only one or two pairs of ovules to each placenta. The ovules arise from the carpellary wall near the roof and become inverted with micropyle upward. The seeds are 3—4 times the volume of those in *F. laevis*.

(5) *F. Boissieri* Reut. in southern Spain; with unusually short tubular portion of calyx, but very long, free tips.

The following more erect bushy shrubs with closely rolled compact leaves usually developing a thick zone of hard bast along the midrib;

(6) *F. corymbosa* Desf.

(7) *F. thymifolia* Desf. incl. *F. Reuteri* Boiss., apparently also *F. pallida* Boiss. et Reut. Numbers (6) and (7) together constitute a rather distinct circle of forms inhabiting more arid localities from southern Spain through Algeria and Marocco into the Sahara.

Frankenia pulverulenta L. possesses the widest distribution of any species in the family, being almost a cosmopolitan coast species, although it has reached the Western Hemisphere only as a ballast plant in recent years. The plant is also widely distributed over the inland salt regions, apparently however fleeing from the driest territory and occurring on the moist saline soil about inland salt lakes. It occurs over the whole of the Mediterranean region northward to the British Isles. Southward to Senegambia and the Canary and Cape Verde Islands and again in Capland; also throughout northern Africa far from the coast. Eastward to Songarei and the Punjab and south-eastward over Arabia.

Noteworthy is the fact that this plant is subject to so little variation throughout the wide region in which it occurs. Except that in certain drier places it becomes more erect and with a somewhat xerophytic aspect, it is always the constant, prostrate, soft, glabrous plant with unrolled, rather fleshy leaves. The wide distribution of this plant is not difficult to explain,

for it produces great abundance of seeds, which find ready escape from the capsule, and being very tiny grains, $^1/_2$ mm in the longer diameter, are easily carried by the wind like light grains of sand, or by coast birds, and so have comparatively free interchange between regions united by coast or sand steppes. As to the relation of *F. pulverulenta* to the Australian and the Chili-Californian regions, a more difficult question of distribution is involved which will be discussed with the corresponding species of those regions.

Concerning the distribution of the polymorphous, shrubby forms of *Eufrankenia* it may be said that two, *F. laevis* and *F. hispida* incl. var. *erecta*, producing many tiny seeds like *F. pulverulenta*, enjoy also a comparatively wide distribution; but they do not possess the capacity for distribution, if one may so express it, of *F. pulverulenta*, which illustrates that other important factors independent of seed production and seed distribution influence the distribution of nearly related species. The other shrubby forms produce for the most part fewer seeds and are restricted to a very local distribution. This difference in distribution capacity between the annual *F. pulverulenta* and the perennial shrubby species lies probably in this very fact of the life period of the individual, wherein is also to be sought the constancy of the one species and the many variations of the other. *F. pulverulenta* is not necessarily associated long with the conditions of any one spot, but springs up, bears its seed quickly and so repeats itself constantly under conditions which are in a sense of its own choosing. The shrubby perennials are, however, not so independent of environment. Slower to find a foot hold they are bound to it permanently and receive in the course of time the effects of imposed conditions. The perennial type has come, ultimately, to a distribution approximately as wide as *F. pulverulenta*, but it has not been able to do so without passing into manifold variations.

In connection with the *Frankeniaceae* of the Mediterranean region two facts deserve here preliminary mention: 1. That throughout this very broad region the species are so nearly related as to fall in the one section *Eufrankenia* (the genus *Hypericopsis* is the one interesting exception). 2. That the species of this region stand in a very intimate relation to a similar development in Australia and the Western Hemisphere.

Hypericopsis.

Hypericopsis persica (Jaub. et Spach.) Boiss. is the one instance among *Frankeniaceae* where the chief distinguishing character is based upon a departure from the type in floral structure unaccompanied by corresponding changes in plant habit. This plant corresponds in vegetative structure to the *F. hispida* var. *erecta* which is also found in south-eastern Persia where *H. persica* is endemic. The constant occurrence of many stamens, 20—24,

and the unusually large flowers — the diameter of the calyx tube at least double that of any other member of the family — are the two noteworthy characters of this isolated genus. It is also worthy of remark that *Hypericopsis* is the only member of the entire Mediterranean region not included in sect. *Eufrankenia.*

In what relation it stands genetically to *Eufrankenia* is not easily determined. The habit of the plant, the method of producing the seed and of allowing them to escape, the number of seed and their charactistics — except their larger size — are all as in the *Frankenia* of the same region. But notwithstanding that circumstances are as favorable for its distribution as for the other forms, the two facts, 1. That it departs widely enough from the type to be called a genus, and 2, that as a genus it is monotypic and narrowly endemic, suggest that *Hypericopsis* should have originated from a prehistoric form rather than from any *Frankenia* of the present day.

2. South Africa.

Turning now to the South African or Capland region we find as already stated that *F. pulverulenta* occupies both the coast and the inland salt lagoon territory. It may be remarked here that neither *F. pulverulenta* nor any other *Frankenia* is known to occur between the Capland and the Senegambian coast. That is to say, the two regions are separated by a zone of over 40 degrees of latitude from which no plants of this family have been reported. It is not surprising therefore, to find that the chief developement of the group is endemic, although indeed, the *Eufrankenia* type appears so strongly as to have led to including the species under *F. capitata* and *F. laevis*, and it is not unlikely that *Eufrankenia* is represented by other forms than *F. pulverulenta.* Nevertheless this region is to be counted with *Occania* rather than *Afra* (strictly it is intermediate between these two), and I would suggest the distinction of the following species:

1. *F. Krebsii* Ch. & Schl. which is very near the *Eufrankenia* type, but although bearing the yellowish seeds of *F. laevis*, these are two or three times the volume of *F. laevis* seeds and the whole plant — the leaves, but especially the flowers — has the more robust build and larger size of section *Toichogonia cosmopolita.*

2. *F. nothria* Thunb., which points to an intimate relation with the Australian and Chilan species of section *Toichogonia cosmopolita* in the very large, long flowers 8—12 mm., correspondingly wider, longer seed capsule, bearing 10—20 seeds, which are oblong reddish brown, more than five times the volume of *F. pulverulenta*, slighthy papillate or with chiefly smooth water-storing epidermal coat.

The South African region possesses no such distinct types as those which characterize the Australian and South American regions.

3. Australia.

Passing next to Australia we find an abundance and variety of forms sufficient to establish this continent as one of the three large centers of developement of *Frankeniaceae*, coordinate with the Mediterranean and South American regions. The species are all endemic and may be included in the genus *Frankenia*, although by no means do they fall within a single type, but on the contrary while developing a marked individuality, the Australian species fall into three groups, the first of which has its counterpart in the Mediterranean region and in Chili; the second in the isolated forms like *F. triandra* Remy of the Puna Region, and *Beatsonia* of St. Helena; and the third in *Niederleinia* of the salt-steppes of Argentine, and *F. Palmeri* and *F. Jamesii* of North America.

Aspreviously stated, the grouping in general is that of »Pflanzenfamilien«. Subgen. *Oceania* stands appropriately for all of the species not found in the Mediterranean region. The genera *Beatsonia* and *Niederleinia* are to be regarded as to their origin as part of this subgenus. Then, instead of only the two sections *Toichogonia* and *Basigonia*, I would suggest a division of *Toichogonia* into *Toichogonia cosmopolita* to include all species of Oceania which correspond to section *Eufrankenia* of subgenus *Afra*, characterized by their much larger flowers and seeds; and *Toichogonia-isolata* to include all the remaining species of Oceania, which, although very widely differing in habit, are bound together by the one character of having very small flowers with ovules formed in the manner of *Eufrankenia*. As suggested in the name, the species in this section are isolated, and sharply defined, having evidently been separated from each other or from a common ancestral type for a very long time.

The genus *Beatsonia* should be reckoned with this section. This leaves sect. *Basigonia* Ndz. unchanged but including also *F. Drummondii* Benth. and *F. tetrapetala* Lab. of Australia. The genus *Niederleinia* stands nearest this section.

Toichogonia cosmopolita.

F. pauciflora DC. occurs in numerous varieties in the characteristic habitats over the whole of the continent and Tasmania [1]), thus corresponding to the shrubby perennial type of *Eufrankenia*. But the most nearly allied species are *F. nothria* of Capland and the shrubby species of sect. *Toichogonia cosmopolita* in Chili. In *F. pauciflora* the flowers are larger than in any other member of the family except *Hypericopsis*, being even of greater length than those of *H. persica*, reaching 12—14 mm with calyx tube 7—10 mm and $1^1/_2$—2 mm diameter. Seeds are produced in abundance as

1) Benth., Fl. Austr. I p. 150.

in *F. laevis*, but are several times the volume of the latter, which fact, however, seems not to have made an appreciable difference in the capacity for distribution. In the matter of plant habit, certain more erect forms of *F. pauciflora* constitute prominent bushy growths of the height of one meter.

Even more interesting because of its relationship is *F. serpyllifolia* [1]) Lindl., placed by BENTHAM as a variety of *F. pauciflora*. *F. serpyllifolia* is an annual prostrate plant exactly corresponding to *F. pulverulenta* of the Med. region and *F. grandifolia* of California and Chili, with the latter of which it coincides strikingly in appearance. But although so nearly related, it is separate from both. The chief distinguishing character is found in the seeds which, have unusually conspicuous epidermal papillae. The seeds of *F. pulverulenta* are very minutely papillate, those of *F. grandifolia* very large, reddish and mostly smooth. While the specimen of *F. serpyllifolia* examined has seeds two or three times the volume of *F. pulverulenta* with papillae half as long as the breadth of the seed itself, which give it a grayish, hairy appearance.

Toichogonia isolata.

This section is represented in Australia by the two species *F. parvula* Turcz. and *F. punctata* Turcz. These are two prostrate shrubby species from West Australia, in which region all of the peculiarly Australian species occur and so far as reported not elsewhere in the continent. Each of these species receives its peculiar distinction from its method of developing leaf structures, which in *F. parvula* are very minute, 1—1½ mm long, of the *Beatsonia* type as to form and manner of folding, but with the peculiar quelling cellulose layer in the epidermis which is most pronounced in *F. bracteata*, but which is developed in most of the strictly Australian type.

The leaves of *F. punctata* are of a form which is not found elsewhere in the family. These occur in isolated pairs at the nodes, where being coalescent, they form an inconspicuous sheath. Instead of having the lamina developed at the upper margin of the sheath the assimilating surface is developed as a lobe-like appendage lying nearly parallel with the stem and closely pressed against it, extending both above and below the surface of attachment to the stem and of coalescence with the opposite leaf.

The floral structure of *F. punctata* is like *Eufrankenia* except that the gynoecium is bicarpellary. Only one or two pairs of ovules are started and probably only two or three seeds matured.

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1) The only specimen I have seen was one collected by MÜLLER in West Austr., which seems to answer to LINDLEY's description of the DRUMMOND specimen from Murchison River. It must have been a plant of this species also which DE CANDOLLE (Prod. I, 350) referred with doubt to *F. pulverulenta*.

Basigonia.

The third group of Australian *Frankeniae* forms a part of the section *Basigonia* Ndz. It is in this section where what may be called the Australian type finds its strongest expression, namely, in the noteworthy species *F. bracteata* and *F. glomerata.*

The method of forming the ovules in sect. *Basigonia* deserves special consideration. From the base of the ovarian chamber there arises for each carpel a single funicular stalk which elongates until nearly reaching the roof, where it makes an arch and continues its growth back toward the base, in the meantime, i. e., after arching, the rudiments of the nucellus and the inner seed coat are apparent at the apex of the funicular growth. With further growth the developing ovule becomes anatropous in the usual manner, but the funicle, beside giving the ovule the half turn and becoming coalescent along one side, also describes the arch above mentioned, and thus the ovule makes one complete rotation, coming finally to lie with the micropyle in the arch of the funiculus a little to one side and pointing to the stylar end of the ovary. In *Niederleinia*, each funicular stalk gives rise to two ovules and so may be considered as two coalesced funiculi, a not improbable case, for in *Eufrankenia* the funiculi arise from the placental surface approximately in pairs.

Important to note is the fact that in this section only one seed, as a rule, comes to maturity. This fact must of course stand in relation with the narrow endemism of the species though not necessarily the chief cause of it.

As indicated previously, the peculiarly Australian *Frankeniae* possess characteristics of leaf structure not found in other regions. This type is the most pronounced in *F. bracteata*, which is the species here described. The plant is a dwarfed shrub, but the internodes are unusually long. Each internode bears a pair of leaves whose coalescent bases form a scarious sheath more or less 3 mm long and ample enough to enclose the fascicles of young leaves in the axils. At first the lamina or assimilative part is articulated to the distal margin of the sheath, but later falls away, leaving the sheath for its protective work. The lamina is unusually long and narrow, very compact, tightly rolled and glabrous. The epidermis is furnished with thick cuticle, and a quelling layer of cellulose, arranged in the peculiar manner of certain species of *Aloe.*

In *F. bracteata* there is a striking peculiarity in the manner of bearing the flowers, which are clustered into an approximate head, well protected by an involucre-like developement of the leaves, which are here not rolled as on the stem, but widely expanded, elliptical in form. In the nearly allied *F. glomerata* the flowers are also in a head, but the encircling leaves

are not expanded. In *F. glomerata* the flowers have reached the minimum of diameter in the calyx tube, which is scarcely 1 mm in diameter, although attaining a length of 8 mm. Coincident with this filiform narrowness of the calyx tube is the reduction of members to $K4 — C4 — A4 — G3$, and the stamens are all of different lengths, allowing the anthers more room for developement within the narrow space.

Relationship of Australian species.

To review briefly, the Australian species of *Frankenia* are all endemic, but they illustrate two very different degrees of endemism:

1. The universally distributed species of section *Toichogonia cosmopolita*, which are so nearly related to corresponding species in the Mediterranean, Capland and Chili-Californian regions, as to suggest a comparatively recent interchange between them.

2. The purely Australian species, which are confined so far as known to the territory of West Australia, the endemic region par excellence of the continent [1]), and which though occurring in sections containing species from the Western Hemisphere, point to a very ancient isolation.

4. South America.

In passing to consider the *Frankeniaceae* of the Western Hemisphere we are confronted with certain conditions whose importance is emphasized in proportion to the isolation of these lands from those we have previously considered. 1. That what has been suggested as the modern cosmopolitan phase of the family recurs in the Western Hemisphere in endemic species with as great abundance and variety of forms as those of the two chief centers previously considered. 2. That of these not one species is found on the whole of the eastern coast of either North or South America (except the introduced *F. pulverulenta* L. in New York Harbor), but confined to those portions of the west coast which lie adjacent to extensive inland arid regions offering favorable opportunity for a varied developement. 3. That the isolated element, the evidently remnant species, occurs here in greater number of species and more extreme types than anywhere else in the world.

As in the Australian species, so in South America there are three sections, two of which are represented in south-western North America.

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1) According to Engler, Entwickelungsgeschichte der Pflanzenwelt II, p. 42 the endemism reaches 80,08 % in West Australia, but only 40,8 % in North Austr., and 43,2 % in East Austr. the next highest centers of endemism.

Toichogonia cosmopolita.

Section *Toichogonia cosmopolita* attains a very marked developement in Chili, corresponding to that of Australia, and Sect. *Eufrankenia* of the Mediterranean region. Reiche and Johow (Flora de Chile I, 1896) enumerate six species with three varieties which would fall in this section: *F. chilensis* Presl, *F. erecta* Gay, *F. glabrata* Phil., *F. Nicoletiana* Gay and vars. *florida* and *aspera* Phil., *F. micrantha* Gay and var. *Berteroana*, and *F. campestris* Schau. Most of these are shrubby perennials very closely allied to *F. pauciflora* of Australia and *F. nothria* of Capland. But at least two, *F. micrantha* and *F. Berteroana*, are *F. grandifolia* Ch. & Schl. The most familiar, and most widely distributed species, *F. Berteroana*, long known from its use as a source of common salt, is pure *F. grandifolia*. *F. micrantha* Gay, should be *F. grandiflora* var. *micrantha* Gay, corresponding to the inland North American *F. grandifolia* var. *campestris* Gay. *Frankenia grandifolia* Ch. et Schl. was originally described as a Californian coast plant. It not only occurs in abundance along the whole of the Californian coast from San Francisco to Santiago, but also in the moist alkali soil of central and southern Calif., extending thence eastward to Southern Arizona, New Mexico, and South to Sonora and Coahuila, Mex. There can be little doubt, however, that the plant originally comes from Chili, where at present it not only possesses a like extensive distribution with that of North America, but stands in the circle of forms of which it is a member, whose developement is peculiar to Chili.

Comparison of sections Eufrankenia and Toichogonia cosmopolita.

If now, we consider the three species *F. grandifolia*, *F. serpyllifolia* and *F. pulverulenta* together, we find a most striking agreement of characters. Each is an annual with mostly plane elliptical leaves, each occurs extensively along the coast and is distributed over the entire floral region to which it belongs. Put together, the three would form a thoroughly cosmopolitan species. Yet one would scarcely say that *F. pulverulenta* with its small flowers and minute yellow seeds, is the same as *F. grandifolia* with its very much larger flowers and especially the large smooth reddish seeds, 8—10 times the volume of those of *F. pulverulenta*, or that either were *F. serpyllifolia* with its gray, hairy seeds. Nevertheless the species are very closely related. Such a striking agreement is not accidental, and the capacity of each for wide distribution also points to a near relationship. Yet in what way are they related? If we should consider *F. pulverulenta* as the parent form we are met by some difficult questions. Above all *F. pulverulenta*, wherever we find it — North Africa, Capland, Songarei, — is the same unvariable plant. Specimens taken from these widely separated

regions could scarcely be distinguished, and although the Chilan and Australian regions offer essentially the same conditions for this unvarying growth that it finds in Capland, their corresponding species are very different. We must suppose therefore, that a very recent interchange between the regions has scarcely taken place. In what way could an interchange occur? The seeds of these plants show no special adaptations for trans-oceanic distribution. They have no means, except their minuteness, by which they would adhere to the feet or legs of coast birds, nor are they likely to prove sources of food for such birds and thus come to a wide distribution as undigested particles.

We must consider further that these species do not stand independently in the regions in which they occur but must be considered a part of the extensive developement of the genus in those regions, so that what has been said concerning the close relationship between the three annual species applies likewise to the shrubby perennials. It has already been pointed out that *F. laevis* in the Mediterranean region becomes a transition form, *F. Krebsii*, in Capland, and that *F. nothria* of Capland has its nearest relation in *F. pauciflora* of Australia. Further, that these two are bound by very intimate characteristics to the common shrubby species of Chili. In fact, then, these four regions, Mediterranean, Capland, Australia, Chili, possess a modern developement of the genus *Frankenia*, each analogous, and nearly related to the other. This repetition of conditions in the different regions points to a facility of interchange entirely inconsistent with the geographical isolation. As indicated, the continuous coast between the Mediterranean and Capland regions can account for the relation of these two, and the same may also be said to account for *F. grandifolia* in California and the adjacent territory. The transoceanic distribution is however quite a different matter, the further consideration of which may be left until the final discussion of the probable history of the *Frankeniaceae*.

Toichogonia isolata.

Those species which are referred to section *Toichogonia isolata* from South America are brought together upon negative characters perhaps as much as upon positive, they are those species which do not belong to *Basigonia* or to the *Toichogonia cosmopolita* groups. As previously stated, the one positive character lies in the floral structure, which in minuteness and in the method of ovule formation is like *Eufrankenia*. Otherwise these species stand sharply distinct from each other both in habit and distribution. They embrace provisionally, *F. triandra* Remy (incl. *Pycnophyllum sulcatum* Griseb. Pl. Lorenz. p. 28) from the Puna Region, *F. farinosa* Remy, northern Atacama, Cobija, placed here from the description, no specimen having been seen, *F. Vidalii* F. Phil., Islands of San Felix and San Ambrosis, *F.*

microphylla Cav., Ic. VI from the Puna Region? and *Anthobryum tetragonum* and *aretioides* Phil. from the Puna Region.

As to the Puna Region: 1. I believe the *F. microphylla* Cav. to be one of the *Caryophyllaceae*, because of its free central placentation, which is a character not found in *Frankeniaceae*. From its habit and floral structure probably *Pycnophyllum*. Unfortunately I have not been able to see a specimen of this plant. 2. *Anthobryum* Phil. first described as a genus of *Primulaceae* is placed with *Frankeniaceae* by Reiche and Johow (Flora de Chile I, 1896). If really one of this family it stands so near *F. triandra* in habit, morphology and distribution that we may, for the purposes of this article discuss them together. This leaves then, *F. triandra* Remy as the type for the Puna Region. Previous to this time, *F. triandra* has been supposed to be confined to the Punas of central Bolivia (Carangas, D'Orbigny; Biacha near La Paz, Weddell Chlor. And.) but the discovery that *Pycnophyllum sulcatum* Griseb. Plant. Lorentz. p. 28, is *F. triandra* [1]) Remy. brings to light a much wider distribution, as well as much new material from which the characters of the species may be more exactly determined. The specimens called *P. sulcatum* were collected by Lorentz and Hieronymus near Congrejo at the northermost boundary of Argentine, and by Lorentz between Laguna-Blancaand Nacimiento Prov. Catamarca.

The two species of *Anthobryum* Phil. were collected in the Puna of Tarapaca, *A. tetragonum* Phil., Polar Grande, *A. aretioides* Phil., Cerro de Copacoya. This indicates a very general distribution throughout the Puna Region.

In its manner of growth *F. triandra* is one of the polster forming plants, common in the high Andean regions. Weddell describes it as forming »plaques arrondies et rayonnantes«. Lorentz speaks of it as occurring in »große Ballen auf salzigen Boden in den Hochthälern zwischen Nacimientos und den Laguna-blanca«. The surface of the polster or mat is a solid mass of vertical branches 3—5 cm long pressed closely together and appearing like mats of moss. The larger, main branches extend almost horizontally, and are entirely buried. In the exposed portions the internodes are very much reduced and the leaves very closely imbricated in four ranks. The flowers are necessarily developed singly and terminal.

The floral structure is normal, i. e., like sect. *Eufrankenia*, except in the number of stamens. There are three in most flowers, but I have found four fully developed anthers in an unopened flower, five and even six

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1) I am very much indebted to the kindness of M. Poisson, curator of Herbarium of the Paris Museum, who through the friendly correspondence of Professor Schumann has sent a small portion of the original plant collected by D'Orbigny, for my examination. From comparison with this specimen *Pycnophyllum sulcatum* Griseb. is found to be *F. triandra* Remy.

filaments in older flowers, but remains of only three anthers. *Anthobryum* Phil. has five stamens. It appears, therefore, that here again the number of stamens is not to be taken for great value in constituting a genus.

The seeds of *F. triandra*, of which so far as examined six or more are matured in each capsule, are some ten times the volume of *F. pulverulenta*, irregular in shape from crowding in the capsule, and furnished with large spherical water — storing cells in the epidermal coat. The capsule before dehiscence is nearly spherical, slighthy wider than long.

Even disregarding the stamen character, we have here a species so isolated from all other *Frankeniaceae* in its vegetative morphology, its form of growth and its distribution, as to merit special distinction which might appropriately be done by elevating it to generic rank as PHILIPPI thought best in describing *Anthobryum*. As touching its phylogenetic relationship this is plain, that the *Frankenia* of the Puna Region has been for a very long time isolated from all other members of the family. This occurrence in such high altitudes (3500—4000 m) is a remarkable exception in the *Frankeniaceae*.

Frankenia Vidalii F. Phil. deserves special interest for two reasons, (1) because of its distribution, (2) because of its relationship. This plant is commonly referred to Chili, but in Flora de Chili it is ascribed to the coasts of the Islands San Ambrosio and San Felix; that is, entirely isolated some 10 degrees west from the Chilan coast. In habit, in the size and occurrence of leaves, in their folding, and the epidermal structure, this plant is more like *Beatsonia portulacoides* than any other species. Although I have not been fortunate enough to examine the flowers, their minuteness — calyx 5 mm long — is further warrant for placing *F. Vidalii* in the section *Toichogonia isolata*. It is, in fact, another one of those species which have evidently been separated from an ancestral form for a very long time. That it should show a nearer affinity to *Beatsonia* of St. Helena than to any Chilan forms seems doubtful, although the southern extratropical islands are not wanting in analogous cases.

F. farinosa Remy is placed with the species of sect. *Toichogonia isolata* provisionally, for it may be only one of the prominent species of sect. *Toichogonia cosmopolita* corresponding to the tall bushy forms of *F. pauciflora* in Australia, but if so, the occurrence of so distinct a species among the South American forms of *Toichogonia cosmopolita* points to a more complex developement of that group than we have been supposing. The plant is described as a woody shrub, growing in dense domelike clusters several feet high (one meter or more?); the branches rigid, covered with a mealy pulverulence; the inflorescence subcorymbose at the apex of branches; stamens five, instead of six as in sect. *Trichogonia cosmopolita*. In isolated lagoons at an altitude of 1000 meters in the mountains about Cobija and northern part of desert of Atacama.

Basigonia.

Section *Basigonia* is not represented in South America so far as known by any species of *Frankenia*, but the genus *Niederleinia* should be considered in connection with this section, of which it is in reality only an extreme form. *Niederleinia juniperioides* Hieron. appears to stand in very much the same relation to the salt-steppes of Argentine that *F. triandra* does to the high Puna region farther north. Each has an extensive distribution in its region, each is the only member of the family in its region, besides, also, these are the two most distinct forms of *Frankeniaceae*, which fact stands in relation with their isolation from other species. But the two forms would seem to have developed entirely independent of each other. The occurence of *N. juniperoides* is described by M. F. KURTZ[1]) as follows: »Die bemerkenswerteste Pflanze dieser salzigen Striche ist jedoch *N. juniperioides* Hieron., ein kleiner, zerbrechlicher, graugrüner Strauch, der im Aussehen ein Diminutivum der in den Gärten als *Juniperus prostrata* Pers. cultivierten Pflanze darstellt. Diese Art, von G. NIEDERLEIN auf den Ufern der Salzsümpfe »Narraco« (nördlich vom Rio Colorado) während der Expedition Rocas zum Rio Negro zuerst gefunden, bedeckt hier eine bedeutende Fläche: von Pendrica am Fuß des Cerro Nevado und der Laguna Llauganelo im Osten, bis zur Junta del Atuel und Agua Nueva im Westen und Norden; sie findet sich in niedrigen, kreisförmigen Gruppen, die bis zu ein Meter Durchmesser besitzen.«

This growing in compact clusters occurs in other species of *Frankeniaceae* as well, e. g., *F. farinosa* Remy, *F. Palmeri* Wats. and others, and one need only imagine it sufficiently reduced and compacted to have the polsters of *F. triandra*.

The vegetation and floral morphology have been well discussed by Prof. HIERONYMUS[2]), and it need only be mentioned here that the leaves are a distinct type with exceedingly thick epidermis, possessing a very prominent quelling cellulose layer; the salt glands are at the bottom of a very deep depression, and the stomata occur only at the bottom of the fold on the dorsal side of the leaf and not at the bottom of the above mentioned depressions as suggested in the description »Spaltöffnungen sehr tief eingesenkt«.

Niederleinia is the only member of the *Frankeniaceae* in which unistaminate flowers are found. The genus appears rightly characterized by NIEDENZU as polygamo-monoecious. In specimens recently received from Dr. F. KURTZ, Cordoba, the stamens have the normal *Frankenia*-arrangement with extrorse-lateral dehiscence of the anthers. In such flowers

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1) Bericht über zwei Reisen zum Gebiet des oberen Rio Salado, aus Abh. Bot. Ver. Prov. Brandenb. XXXV.

2) Botanical Report of the Roca »Expedicion al Rio Negro« 1881.

the ovules are exactly as in the pistillate, but very little if any stigmatic surface is developed and probably no seeds mature. The ligule of the corolla is also quite as plain as in many species of *Frankenia*.

The method of forming the ovules has already been sufficiently discussed with the Australian species of sect. *Basigonia*. Since only one seed comes to maturity, and since many flowers probably have only an abortive ovary, the seed production in *Niederleinia* would seem to have reached the minimum. Such species appear to be on the decline, and it is not unlikely that the occurrence of unistaminate flowers is but an indication of decline in the reproductive capacity.

5. North America.

Toichogonia cosmopolita.

There are in North America three species of *Frankenia* of which *F. grandifolia* Ch. & Schl. and var. *campestris* Gray, sect. *Toichogonia cosmopolita* have been already sufficiently discussed. The two remaining species belong to the following section.

Basigonia.

F. Palmeri Wats. has been found in salt marshes about Sandiego Bay, at National City, and on the East Coast of Lower California. It occurs as a compact densely branched shrub, of very pronounced xerophytic habit. In the floral parts, *F. Palmeri* is irregular in the number of stamens. There may be four or five of these. The carpels are regularly two, and only two ovules are formed. The leaves are noteworthy from the enormous developement of sclerenchym a cells along the course of the small vessels throughout the lamina. Coincident with this is the fact that the leaves are not so compact and the epidermis not so thick as in most species of correspondingly xerophytic habit. In the latter the mechanical tissue is in the form of true bast or libriform cells along the midrib.

F. Jamesii Torr. has the following distribution according to A. Gray [1]). Eastern foot of the Rocky Mountains in Colorado, especially on the Arkansas River; Guadeloupe Mountains, western Texas. The flowers of *F. Jamesii* are normal in the number of parts, $K5 — C5 — A6(3—3?) — G3$; style 3-cleft. The calyx tube is very long and narrow the corolla lobes also narrow as in the Australian species of this section. As in these also, the leaves of *F. Jamesii* are long and narrow, the epidermis however of very large, comparatively thin walled cells.

Both genetically and geographically *F. Palmeri* and *F. Jamesii* are very distinctly separated.

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1) *Frankeniaceae,* Synopt. Fl. No. Am. Vol. I pt. I fac. I p. 208.

Relation of North American species to other regions.

It has already been stated that *F. grandifolia* must undoubtedly be Chilan in its origin and that the continuous coast line between Chili and California would be sufficient to account for the means of distribution in general. Whether this occurred step by step along the coast or whether coast birds carried the seeds by long flights across the equator to the extra-tropical regions north may not be decided. From the entire absence of special mechanism for distribution the former method would seem the liklier. But in as much as the species has attained such a wide distribution into isolated basins shut off by mountains from the Californian coast, even to salt lakes 1200 m above the coast, the agency of birds would seem necessary.

With *F. Palmeri* and *F. Jamesii* the case is entirely different. *F. Palmeri* might occupy the same relation to Chili that *F. grandifolia* holds, from its position on the coast, but thus far no species of this section has been found in Chili. This relation could not, however, hold for *F. Jamesii*, which has no connection either with the coast or with the basin desert territory eastward. These are therefore, two more of the sharply defined isolated species. Their congeners are *F. bracteata*, *F. glomerata* and two or three other species from the endemic region of West Australia, the most pronounced types of that continent, and *Niederleinia juniperoides* from the salt-steppes of Argentine, a still more extreme type. As stated in the introduction to this article, the geographical conditions preclude the possibility of a direct transportation of seeds between these regions. It is more probable that section *Basigonia* has at some time possessed a more general distribution than it now has. This question will be further discussed in part III of this article.

6. Oceanic Islands.

In addition to the inland salt-steppes and the coasts above considered, certain groups of islands also possess species of *Frankeniaceae*:

(1.) The Cape Verde and Canary islands, which contain only *F. laevis* with some marked variations from the common Mediterranean form.

(2.) The Island of Tasmania, which possesses the wide spread Australian *F. pauciflora*.

(3.) Islands of San Felix and San Ambrosio, which contain a marked endemic species, *F. Vidalii*. This was described with the South American species.

(4.) The Island of St. Helena. This island contains the monotypic genus *Beatsonia*.

Beatsonia portulacoides Roxb. is no doubt rightly considered one of the indigenous plants of St. Helena, having been first collected by Beatson in 1813. This is the more certain in as much as the genus does not occur

elsewhere. It is very remarkable, however, to find a member of the *F.* in this isolated island, which, having retained so little modified the characters of typical *Frankenia*, is still so distinct from forms now living. Particularly is there no species in the adjacent continent of Africa from which it could have originated, and the only species in the family which shows a striking agreement with *B. portulacoides* is *F. Vidalii* from the islands San Felix and San Ambrosio some 10° West of the Chilan coast about 26° South Latitude. The distinguishing characters of *Beatsonia* are anatomical rather than morphological. The floral structure is not like normal *Eufrankenia*, but it does not depart further from this than several other species of *Frankenia*. But among plants which have to adapt themselves to very severe conditions — as in the case of halo-xerophytic groups — the more significant characters may well have expressed themselves in the vegetative structure, particularly in the assimilative organs, where as a consequence we have in *Frankeniaceae* several distinct types of leaves, based on the form, the occurrence on the stem, and the anatomical structure.

III.

Comparison and grouping of the sections considered in II, and speculation as to the probable history of the Frankeniaceae.

We have found from the foregoing examination of species that two very different conditions prevail in this family.

1. A very abundant and extensive developement of the family which has filled most of the great salt desert regions of the world with a large number of forms, closely intergrading in the same region and nearly related in the different regions. That is, a present developement of one common type embracing *Afra-Eufrankenia* and *Oceania-Toichogonia-cosmopolita*.

2. A large number of monotypic forms occurring in most isolated locations entirely disconnected from the above group, and sharply defined from each other. That is to say, by all their conditions pointing plainly to the fact that they represent the ends of branches, so to speak, the remnants of a previous developement of the family. Embracing *Oceania-Toichogonia isolata* and *-Basigonia* and the genera *Beatsonia*, *Niederleinia* and *Hypericopsis*.

Group 1.

We have seen concerning the first group, that in view of the very close relation between species of the different regions, a distribution from one to the other must have occurred within comparatively recent time; not so recent, however, but that endemism prevails as between regions separated by a broad stretch of ocean.

It was mentioned earlier as a notable circumstance that no species of *Frankeniaceae* occurs on the Atlantic coast of North or South America (except the introduced *F. pulverulenta* in New York Harbour). Likewise noteworthy is the lack of any representative of the family in the Eastern Asiatic salt deserts, or on the east Asiatic coast, so that a distribution from the Mediterranean region to the Western Hemisphere has probably not occurred. Much more is it likely that the distribution has proceeded from Australia to the American continent reaching naturally, the nearest region, the Chilan coast, first, which is born out by the strikingly close relationship of *F. serpyllifolia* Australia to *F. grandifolia* Chili and of *F. pauciflora* Australia to *F. chilensis*, *erecta*, *glabrata* etc. of Chili.

It seems also probable, from the very extensive developement in Australia that *F. nothria* of Capland is of Australian origin, and that in the Capland region we have the meeting of Australian and Mediterranean elements.

Whether now the original center from which all of this modern developement arose was the Mediterranean region or the Australian, is not easily determined, if at all possible.

Three facts speak in favor of a southern extratropical origin.

1. The lack of *Frankeniaceae* on the East American coasts or in the East Asiatic salt-steppes.

2. The predominance of only the closely related species of the modern developement in the Mediterranean region, and conversely.

3. The abundance of monotypic isolated forms in the southern extratropical regions.

Whatever may have been the direction of distribution, we must conclude that by some means, seeds of *Frankenia* have been carried over the regions between Australia and the Capland, and between Australia and the western South American coast.

If the previous interpretation of the relation of species be correct, a distribution by means of shipping would not allow sufficient time for the varied developement within the regions.

It is impossible that such a distribution could be made by means of ocean currents, if for no other reason than that the seeds themselves are tiny grains which quickly sink in water.

Further, the seeds are in no way adapted for clinging to objects, nor are they apparently food for any birds which are coast frequenters and at the same time birds of long flight, and yet there is this small chance, that in some accidental way they might remain attached to the body or in the alimentary canal of one of those birds which are able to remain on the wing for days at a stretch, and could, so far as the mere ability is concerned, make the flight between Australia and the Capland or Chili.

That other plants have attained a distribution over those same stretches

of ocean is an accepted fact. One need only recall the case of *Pelargonium* of South Africa, of which two very nearly related species occur in Australia concerning which Prof. ENGLER (Geogr. Verbreit. d. Zygophyll. S. 21) says, »kaum daran zu zweifeln ist, dass das Auftreten von *Pelargonium* in Australien auf transoceanischen Transport von Samen aus Südafrika zurückzuführen ist«.

One can only speculate as to the particular method by which the transportation has been accomplished, but this remains evident, that in *Frankenia* there has occurred more than a single, accidental case of transportation at a time when the geological conditions were practically as they are now.

Group 2.

In the second group the species and their distribution are as follows:

1. *Hypericopsis persica,* — South Eastern Persia.

Toichogonia isolata.

2. *Frankenia punctata* and *parvula,* — West Australia.
3. *F. triandra* {*Anthobryum*}, — Puna Region of So. America.
4. *F. Vidalii,* — Pacific Islands of San Felix and S. Ambrosio.
5. *F. farinosa,* — Northern part of Desert of Atacama.
6. *Beatsonia portulacoides,* — Island of St. Helena.

Basigonia.

7. *F. bracteata* and others, — West Australia.
8. *F. Jamesii,* — Eastern foot of Rocky Mountains to W. Texas, No. Amer.
9. *F. Palmeri,* — Lower California, No. Amer.

10. *Niederleinia juniperoides,* — Salt-steppes of Argentine, So. Amer.

This group embraces three, possibly four, monotypic genera, and six other forms so isolated and so distinct that we may regard them also as monotypic branches. The only exception to this condition of things is that in western Australia sect. *Basigonia* has at least four nearly related species.

These conditions indicate that there has not been an interchange between the regions, but rather that each type has reached its present state within the region it now occupies. It is out of the question that seeds should be transported from Australia to the Argentine salt-steppes, or to the lower Californian coast, above all to the eastern base of the Rocky Mountains, yet section *Basigonia* occupies all these regions, and singularly enough, the Australian and North American species are much nearer in their relation to each other than either to *Niederleinia.* It is equally difficult to believe that there has been a transportation of seeds between western Australia, the Island of St. Helena, and the Puna Region. It seems more probable and entirely within the bounds of reason to suppose that the forms in this second group constitute the remnants of a developement of *Frankeniaceae* which in an earlier period possessed a wide distribution over

salt-steppes and along sea coasts very different in their extent and position than those of the present time. The present conditions point to the southern continents as being the area of this developement, and it may be that in western Australia where the two branches *Toichogonia isolata* and *Basigonia* meet, the former with two species, the latter with four or more, we have still a modern coherent portion of the developement. It is not necessary to suppose that all of the regions which now contain the remnants, were at that time connected by salt-steppes or even by coast lines, but we know that after the Tertiary period, the land newly reclaimed from the sea, and therefore presumably fit only to sustain a halophytic vegetation, would, in South America for example, have reached far to the north of the present location of the Argentine salt-steppes. It is entirely possible that species like *F. Palmeri* on the lower Californian coast, *F. Vidali* on the islands of San Felix and San Ambrosio, *Beatsonia* on St. Helena, owe their existence there to a transportation of seed from some other region, but not from the regions which their congeners now occupy.

The entire absence of these isolated elements in South Africa, indeed from the whole of Africa, is noteworthy. Their prevalence in Australia and extratropical South America suggests a closer relation of these continents geographically than exists at present. The distribution coincides to a noticable extent with that of the Old Oceanic Floral elements, and one may be allowed the speculation whether the nearer relation between Australia and South America could have occurred for the *Frankeniaceae* in the existence of a more northerly reaching coast of the Antarctic continent. This would necessitate the supposition that a very much milder climate prevailed than now, in as much as the *Frankeniaceae* grow only in tropical or subtropical climates, and the hypothesis is even more untenable because the old Oceanic floral element contains no halophytic groups.

Any further statements than the facts of distribution and of evident genetic relationship are necessarily hypothetical. The following propositions are, however, offered as being to a reasonable degree supported by the facts of distribution and relationship:

1. That there existed a prehistoric developement of *Frankeniaceae* identified in its distribution with the then existing salt — steppe and coast lands, particularly of the southern continents.
2. That the present sections *Toichogonia isolata* and *Basigonia* with the genera *Beatsonia*, *Hypericopsis* and *Niederleinia* are elements of this former developement, which exist as isolated remnants.
3. That sections *Eufrankenia* and *Toichogonia cosmopolita* are an element originating from the earlier developement, but distinguished by their great capacity for multiplication and distribution.
